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A NEW MENDELIAN RATIO AND SEVERAL TYPES OF LATENCY

DR. GEORGE HARRISON SHULL

STATION FOR EXPERIMENTAL EVOLUTION OF THE CARNEGIE INSTITUTION, COLD SPRING HARBOR, N. Y.

INTRODUCTION

IN two papers presented before the Botanical Society of America at its annual meetings in New Orleans (1905) and New York (1906), I discussed the question of latency as exemplified by certain color-characters in common garden beans (*Phaseolus vulgaris*). These papers were published in reversed order in SCIENCE, May 7 and 24, 1907.

It was shown that certain characters appeared in the hybrids, of which no indication was found in either parent, and the origin of these novelties was traced to unseen Mendelian units possessed by the white bean (White Flageolet) used in the various crosses. The new characteristics were a mottled color-pattern, *M*, and a blackener or enzyme, *B*, which acts upon brown or yellow pigments, *P*, to produce anthocyan, the presence of the latter resulting in black or various shades of violet to reddish purple seed-coats. It was assumed that the brown and yellow beans used in these crosses have the gametic formula, *Pbm,* the black bean the formula, *PBm,* and the white the gametic formula, *pBM*. In crossing the white bean with any of the self-colored beans the three dominant units were brought together, resulting

in a purple mottled F_1 (*PBM*). It was the occurrence of this purple mottled F_1, no matter which pigmented bean was used, that led to my conclusions regarding the latency of a mottled color-pattern and a melanizer in the white bean, and also to the prediction that F_2 would consist of the five forms—purple mottled, black, brown mottled, brown (more properly, dark orange), and white, —in the well-known tri-polyhybrid ratio, 27 : 9 : 9 : 3 : 16.

An Unexpected Ratio and its Significance

At the time my last report was made, the count of the F_2 hybrids had not been completed, but the five predicted types were clearly presented. On summing up the results of the census of the numerous F_2 hybrid families, it was found that the ratio was not as predicted, but the mottled and self-colored beans occurred in all cases in approximately equal numbers, resulting in the ratio 18 : 18 : 6 : 6 : 16, or, reduced to its lowest terms, 9 : 9 : 3 : 3 : 8. To be exact, in the cross between Ne Plus Ultra (dark orange yellow, called "brown" in my notes) and White Flageolet, 10 families gave 133 purple mottled, 114 black, 40 brown mottled, 50 brown, 105 white, and 6 doubtful. Similarly, in the cross between Long Yellow Six Weeks (light yellow) and White Flageolet, 13 families gave 154 purple mottled, 159 black, 39 yellow mottled, 59 yellow (or brown), 160 white, and 12 unclassified. In the cross between Prolific Black Wax and White Flageolet, 3 families gave 53 purple mottled, 59 black, 44 white and 4 unclassified.

On comparing these results with those published by Tschermak[1] it is found that they are in perfect accordance with them, as he also found in a number of similar crosses, an equality between the mottled and self-colored beans. But our conclusions were diverse as to the source of the mottled pattern, I assuming that the mottled factor was brought into the combination by the white

[1] Tschermak, E. Weitere Kreuzungsstudien an Erbsen, Levkojen und Bohnen. *Zeitschr. Landw. Versuchsw.*, 7, pp. 533–638, 1904.

bean as a simple Mendelian unit, while he assumed that a mottled factor was carried as a "cryptomere" by the pigmented bean and that the white bean acts simply as a releasing agent or activator which allows or compels the latent mottling to become apparent.

The ratio 18:18:6:6:16 must have at first a very unfamiliar look to the student of genetics. It was not explained by Tschermak, but was separated by him into two groups of 9:3:4, wherein the interrelations of the several terms need no explanation.

The census of my second generation was completed shortly after the appearance of De Vries's[2] interesting account of "Twin hybrids" in Œnothera, and the suggestion lay at hand that this ratio presented by Phaseolus might be a case of twin di-hybrids, the first and second terms of the ratio, as also the third and fourth terms, being in each case different phases or aspects of a single unit, which might be expressed thus 9A:9∀:3B:3ꓭ:8W. While such an hypothesis would fit the conditions presented by the F_2, it was seen very soon that it does not harmonize with the occurrence of a uniformly purple mottled F_1, nor with the splitting phenomena of F_3, a portion of which has been already examined. A consideration of the F_1 and F_3 shows that there are three distinct units involved, as was stated in my earlier papers, namely—a pigment factor, *P*, a blackener, *B*, and a mottled pattern, *M*.

If all of these characters behaved according to the simple Mendelian method, the ratio would be that previously predicted, and out of every 64 individuals, on an average, 27 would have purple mottled seeds, and 9 black. In order that the number of individuals having purple mottled seeds shall be equal to the number having black seeds, it is necessary that of the 27 that should on theoretical grounds be purple mottled, 9 must show no purple mottling but must be black, though it contains the dominant mottle factor, *M*. This group of 27 purple mottled

[2] De Vries, H. On Twin Hybrids. *Bot. Gaz.*, 44, pp. 401–407, D 1907.

individuals belonging to the theoretical F_2 ratio consists of the following eight types:

1 *PBMPBM*
2 *PBMPBm*
2 *PBMPbM*
2 *PBMpBM*
4 *PBMPbm*
4 *PBMpBm*
4 *PBMpbM*
8 *PBMpbm*
27

There is only one basis on which a group of 9 individuals having a common gametic feature may be derived from this group, namely, on the ground of homozygosis with respect to any single allelomorph. Thus, there are 9 homozygotes with respect to *P* (1 *PBMPBM* + 2 *PBMPBm* + 2 *PBMPbM* + 4 *PBMPbm*), 9 homozygotes with respect to *B* (1 *PBMPBM* + 2 *PBMPBm* + 2 *PBMpBM* + 4 *PBMpBm*), and 9 homozygotes with respect to *M* (1 *PBMPBM* + 2 *PBMPbM* + 2 *PBMpBM* + 4 *PBMpbM*), and the assumption that any one of these groups will give self-colored beans will answer the requirements of the empirical F_2 ratio, 18:18:6:6:16.

The only way in which it is possible to decide which of these three possible groups of 9 homozygotes is responsible for the equality of the mottled and self-colored types is to test their applicability to the other generations, since they all fit equally well the ratio found in the second generation. If homozygotes with respect to *P* hide the presence of *M*, it will be impossible to find an individual with mottled seeds which will not give a progeny, one fourth of which will be white-seeded; but of the F_3 families already examined, a number have been found which, while continuing to give mottled and self-colored beans in the ratio 1:1, have failed to produce any whites. If the homozygotes with respect to *B* are responsible for the latency of *M*, some brown or brown

mottled offspring would be produced by every purple-mottled parent, and there would be no equality between the purple-mottled and black in many families of the third and subsequent generations; but those F_3 families which have been thus far investigated show a number of instances in which purple mottled parents produce no brown or brown mottled young and there is a continued equality between the mottled and self-colored offspring of such parents. The remaining possibility, namely, that individuals which carry the mottled pattern, *M*, but are homozygous with respect to that character, are not mottled but self-colored, is the only one that fits all of the observed facts. The mottled color-pattern must be heterozygous in order to become apparent in the hybrids.

We may then indicate the composition of the group of individuals of F_2 which carry the dominant mottling factor, *M*, and the expectation as to the composition of the offspring which each will produce in F_3 as follows:

1 *PBMPBM* = Bl(Bl) (*M* latent in all).
2 *PBMPBm* = PM(1PM:1Bl) (*M* latent in ½ the Bl).
2 *PBMPbM* = Bl(3Bl:1Br) (*M* latent in all).
2 *PBMpBM* = Bl(3Bl:1W) (*M* latent in all).
4 *PBMPbm* = PM(3PM:3Bl:1BrM:1Br) (*M* latent in ½ the self-colored).
4 *PBMpBm* = PM(3PM:3Bl:2W) (*M* latent in ½ the Bl and ¾ the W).
4 *PBMpbM* = Bl(9Bl:3Br:4W) (*M* latent in all).
8 *PBMpbm* = PM(9PM:9Bl:3BrM:3Br:8W) (*M* latent in ½ the self-colored and ¾ the W).

It will be seen from this scheme that the mottled color-pattern could exist and does exist as a latent (*i. e.*, invisible) character in pigmented beans just as well as in the white bean, which is contrary to the assumption made, when I insisted that the mottled pattern must have come from the white bean. It is also obvious that the mottled

pattern could not exist in both the pigmented and white beans used in these crosses, as in that case the F_1 hybrids would have been homozygous with respect to this character and would have been black self-colored instead of purple mottled. In attempting to settle the question as to the origin of this mottled color-pattern I have carefully examined the results recorded by Tschermak and find evidence that at least one pure-bred pigmented bean must possess the mottled pattern while another does not. Whether the white beans used by him carried latent *M* can not be settled at present, but it is now plain that he may have been right in referring the mottling factor to the pigmented beans. My White Flageolet as well as all the white beans used by Tschermak may not have the mottled pattern, and the gametic formula of the White Flageolet should then be written *pBm*, instead of *pBM*.

This question can only be settled by further careful crossing. The evidence derived from Tschermak is as follows: In the cross between "Hundert für eine" (light yellowish brown) and "Mettes Schlachtschwert" (white) there was no mottling in the offspring; "Hundert für eine" crossed with "Schwarze Neger" (black), both self-colored, gave mottled offspring. Now according to my hypothesis, if "Schwarze Neger" carries the mottled pattern, "Hundert für eine" does not have it, and in turn, "Mettes Schlachtschwert" must not have it. If "Schwarze Neger," on the other hand, does not carry the mottled pattern, "Hundert für eine" has it, and in this case "Mettes Schlachtschwert" must also carry it. We can not say certainly, therefore, that the white "Mettes Schlachtschwert" does or does not have the mottled pattern, but on theoretical grounds either condition would be equally possible.

Among the corollaries of the explanation here given for the ratio 18:18:6:6:16 is not only the fact already given that the mottled pattern may be carried by the pigmented bean invisibly quite as well as by the white bean, but also, since the mottled beans are heterozygous with re-

spect to *M*, it would be impossible to have any of them breed true, *i. e.*, the mottled bean is in the same category in this respect as the famous Blue Andalusian fowl. This conclusion is supported by 48 families of the third and fourth generations reported by Tschermak and by over sixty families of the F_3 from my own mottled hybrids which have been already examined. Not one instance has been found in which the offspring of a mottled hybrid were even approximately all mottled.

The existence of pure-bred mottled races raises the interesting question as to what relation exists between these mottled hybrids which are heterozygous and can not breed true and the true-breeding mottled varieties. Tschermak[3] shows that in crosses between constant mottled races and self-colored races, the mottled pattern acts as a typical Mendelian dominant, the hybrids splitting in F_2 and subsequent generations in the ratio, 3 mottled : 1 self-colored.

Latency due to Separation

With respect to the question of latency since the purple mottling may not be a latent character of the White Flageolet, the type of latency discussed in my previous papers was only certainly exemplified by the pigment-changer, *B*, carried by the white bean. This type of latency is discovered by the production of a novelty when two allelomorphs are brought together, one or each of which, when acting alone, produces no visible character. Thus the black or purple color of these hybrids is due to the combination of the yellow or brown pigment of the pigmented parent and the colorless pigment-changer borne by the white parent. It may be called *latency due to separation* since patency is brought about by recombination. In my first paper on latency,[4] issue

[3] *Loc. cit.*

[4] Shull, G. H. Some Latent Characters of a White Bean. *Science*, N. S., 25, pp. 828–832, May 24, 1907.

was taken with Lock[5] regarding his assumption that novelties which appeared in crosses between certain peas were due to inactive units which became active on crossing. Lock[6] has since reconsidered that case and independently come to the same conclusion that I reached, namely, that the spotted seed-coat was introduced by the white-coated pea in which it was invisible owing to its separation from the pigment-producing factor. This is not an uncommon type of latency and seems to be the only type included by writers who have treated the subject of latency from the Mendelian view-point. It gives rise to such modifications of the Mendelian ratios as 9:3:4, 9:7, 27:9:9:3:16, 27:9:28, etc., instead of the theoretical 9:3:3:1 and 27:9:9:9:3:3:3:1. Some of these modified ratios are of more common occurrence, and are more familiar, than the unmodified ones, perhaps owing to the fact that albinism has been so frequently involved in the Mendelian investigations. Characteristics which are rendered latent by separation in the course of Mendelian hybridization have been called "masked" characters by Punnett.[7] This is not a particularly apt term for latent characters of this type, and would be much more appropriately applied to cases of latency due to hypostasis discussed below.

LATENCY DUE TO COMBINATION

The existence of mottling as a latent characteristic in pigmented beans, due to the fact that it only becomes apparent when in the heterozygous condition, is obviously of an entirely different type. Instead of being a phenomenon of separation, it is due to the union in the same zygote, of two dominant allelomorphs, either of which alone will produce a manifest character, but

[5] Lock, R. H. Studies in Plant Breeding in the Tropics. *Ann. Roy. Bot. Gard. Peradeniya*, 2, pp. 299–356, 1904. See p. 241.

[6] Lock, R. H. On the Inheritance of Certain Invisible Characters in Peas. *Proc. Roy. Soc.*, B, 79, pp. 28–34, 1907.

[7] Punnett, R. C. Mendelism. 2d ed., pp. viii + 85, 1907, London: Macmillan & Co. See pp. 47–53.

which, when acting together, produce none. This may therefore be called *latency due to combination,* since patency is brought about by separating the two allelomorphs whose union effaces their characteristic manifestation. If the White Flageolet carries the mottling factor, *M,* as was at first supposed, the appearance of mottling as a novelty in the first generation hybrids was due not alone to that fact, but just as much to the fact that the pigmented bean does not carry the mottled factor; or if, on the other hand, it should prove true on further investigation that the white bean does not carry the mottled factor, the mottled F_1 is due to this very fact, quite as much as to the fact that the colored bean does possess it.

The conclusion, reached in my previous papers, that the primitive bean was probably purple mottled and that the purple mottled condition is therefore an atavistic one, seems to be left in some doubt, because of the existence of two types of mottling, one of which behaves as a typical Mendelian unit as shown by Tschermak, the other having the peculiar faculty of losing its external manifestation the instant it becomes homozygous. I have no doubt that in some form the mottling unit is a primitive one, but whether the ancestral bean possessing that unit was mottled or self-colored would depend entirely on which type of the mottling unit it carried. In order to breed true it is necessary that both eggs and sperms shall all carry the mottled factor, and if this mottled factor were of the latter type, the beans produced by the union of such sperms and eggs, being homozygous with respect to mottle, would be self-colored, while if the mottle was of the former type, the homozygous beans would be mottled. The conclusion as to the allelomorphic composition of the original bean is probably correct, but as to its external appearance, it may as well have been black as mottled.

The peculiar behavior of the purple mottled allelomorph in my hybrids and in most of Tschermak's, may have a

very important bearing upon the interpretation of what are known as mid-races, *i. e.,* races which regularly produce two forms in about equal proportions, for, as has been seen, the mottled beans of all the hybrid families which did not have a mottled bean as one of its original pure-bred ancestors, constitutes a mid-race. This fact was recognized by Tschermak (*loc. cit.,* p. 47), though he attributed it to an unexplained effect of cross-fertilization, and not to the characteristic behavior of a definite Mendelian allelomorph. Other mid-races may likewise represent instances of latency due to combination. Wherever there is a double series of characters occurring in about equal numbers in the progeny of a self-fertilized individual, this type of latency should be looked for.

Purple punctation and brown flecking, which occur as novelties in the seed-coats of hybrid peas, were found by Tschermak to behave in a manner quite analogous to the mottling in beans, the first generation showing dominance of the novelty and subsequent generations always splitting into the punctate and non-punctate or the flecked and unflecked, respectively, and these no doubt are also cases of latency due to combination. Lock[8] has shown, on the other hand, that when certain mottled and spotted peas are crossed with self-colored peas, the mottling and spotting act as typical Mendelian dominants capable of extraction as characteristics of pure-breeding races, which ought to be expected, since the homozygous parental strains possessed these characters. The apparent discrepancy between his results and those of Tschermak will be fully explained if we assume that there are two types of these color-pattern characters in peas, as there are in beans.

In all of these cases of latency due to combination, the two units involved are of the same kind, so that the latency occurs only in the homozygous individuals, thus resulting in a striking contrast between homozygotes and

[8] Lock, R. H. On the Inheritance of Certain Invisible Characters in Peas. *Proc. Roy. Soc.,* B, 79, pp. 28–34, 1907.

heterozygotes. There are many other cases in which the homozygote and heterozygote show marked and often unexpected differences, the case of the Blue Andalusian fowl being one of the best known of these, but the heterozygous type of the Blue Andalusian fowl or other similar forms is not a case of latency at all, since no hidden allelomorph is brought to light as a result of heterozygosis, but only an unexpected external manifestation.

Latency due to Hypostasis

A third type of latency has also appeared in these bean hybrids, as best exemplified by a cross between the Prolific Black Wax and the Ne Plus Ultra, and between Prolific Black Wax and Long Yellow Six Weeks. In both of these crosses, besides the black and orange or black and yellow which were expected in the ratio 3:1, there have appeared a considerable number of beans of a dark seal brown or a dark greenish brown color. It is certain that these dark brown beans owe their color to the latency of a dark brown factor in the black bean. It has not been an infrequent occurrence to find black beans, not quite perfectly matured or which have been more or less weathered, that show this brown color apparently underlying the black. In this case the appearance of the novelty is due to the presence of a characteristic which can not be seen (*i. e.*, which is latent), for the simple reason that the black pigment possessed by the same bean is so intense as to cover over and hide the brown pigment. The independence of the brown and black pigments allows them to be separated into different individuals upon crossing the black with some other color.

Letting D represent this dark brown factor, the gametic formula for the black bean is BD, and for the orange brown and yellow beans, bd. This assumption leads to another rather unfamiliar modification of the Mendelian ratio, since the F_2 should consist of black, brown and orange or yellow in the ratio 12:3:1. The actual ratios are in essential accord with this expectation though there

are rather wide discrepancies due to the fact that the categories were not as carefully distinguished at first as they should have been. Thus in the case of the cross of Prolific Black Wax (black) with Ne Plus Ultra (dark orange or "brown") many of the dark brown beans were recorded at first simply as "brown," and the ratio found, 174 black:47 seal-brown:26 "brown," shows clear evidence of the extent of error thus produced. A deficiency of black is also apparent and is no doubt due to the recording of some weathered blacks, as dark brown. In the cross between Prolific Black Wax and Long Yellow Six Weeks, the deficiency in the blacks and corresponding excess in the dark brown is even more striking, giving the ratio, 155 black:55 dark brown:9 yellow:5 unclassified, theory requiring 168 black:42 dark brown:14 yellow. This factor *D* is also found to be present in the White Flageolet, where, like the black factor, *B*, it is latent by separation.

The occurrence of dark brown as an invisible character in the black bean may be called a case of *latency due to hypostasis,* following the terminology suggested by Bateson.[9] The unexpected character is not inactive, but its characteristic manifestation is invisible because it is hidden or inhibited by some other quality, and can only become visible when the overlying or inhibiting quality is removed by some means.

This type of latency is no doubt very common, as it is involved in many cases of simple dominance, as that term is generally understood. If the "presence and absence" hypothesis has general validity (and there is a very great preponderance of evidence in favor of it), the term "dominance" should be limited to the relation of the presence of any characteristic to the absence of that same characteristic, and should not be used for the relation between two different positive allelomorphs by virtue of which one hides the presence of the other. Bateson

[9] Bateson, W. Facts Limiting the Theory of Heredity. *Science,* N. S., 26, pp. 649–660, November 15, 1907.

applies the terms "epistatic" and "hypostatic" to the relative capacity of one unit to hide or to be hidden by another, owing to what I call latency due to hypostasis. As a simple illustration, a cross between a pea with yellow cotyledons, Y, and one having green cotyledons, G, shows Y dominant over its absence, y, and not over G. This would become immediately obvious if we could cross the yellow pea with still another type, say with one having colorless cotyledons. The correct gametic formula for the yellow pea is not Y but YG, in which the green is latent owing to the fact that Y is epistatic to G. The gametic formula of the green pea is yG.

That this is a correct interpretation of the apparent dominancy of one positive allelomorph over another is shown by some of my bean crosses. Thus Ne Plus Ultra (dark orange yellow) crossed with Long Yellow Six Weeks (light yellow) produced in 14 F_2 families, 382 orange yellow:130 light yellow, an apparent dominance of orange over light yellow. That the light yellow is latent in Ne Plus Ultra and is not the recessive condition of the orange yellow allelomorph is proved by the fact that in the F_2 families of the cross between White Flageolet and Ne Plus Ultra, light yellow beans appear. Letting O represent the orange allelomorph and Y the yellow one, the gametic formula of Ne Plus Ultra with respect to these two factors is OY, that of the yellow bean is oY, and that of the white bean likewise oY.

The ratio, 12:3:1, presented by the crosses of Prolific Black Wax with Ne Plus Ultra and Long Yellow Six Weeks, has been reported for but one other case so far as I know, though it ought not to prove very uncommon. It will appear in the F_2 of any cross which produces an F_1 of the form $ABCab$ with B hypostatic to A, C hypostatic to both A and B, and neither A, B, nor C latent from any other cause. In these beans the crosses are of the type $ABC \times abC = ABCab$, *i. e.*, both B and C are latent in the one parent and no latent characters are demonstrated in the other. The same ratio will result from a

cross of the type $AbC \times aBC = ABCab$ provided the same relations exist among the several allelomorphs as before. In this case the character C is latent by hypostasis in both parents. This condition has been realized by Toyama[10] in hybrids between the common Japanese white silk-worm and the Siamese striped silk-worm in both of which a "pale," unmarked type is latent by hypostasis. The F_1 is uniformly striped like the Siamese, and the F_2 consists of striped, "white," and "pale" in the ratio 12:3:1. Toyama's statement that the "pale" character was in the "dormant" state indicates a misconception of the nature of latency due to hypostasis.

LATENCY DUE TO FLUCTUATION

Another very potent cause of latency is to be found in fluctuation. It is well known that many of the less marked qualities of plants do not appear under unfavorable conditions of growth. By growing the offspring of these poorly developed individuals under favorable conditions they may be shown to possess all the characters of other members of the race to which they belong. Invisibility produced by this cause may be called *latency due to fluctuation.* Patency is brought about by good feeding, room for full individual expression, etc. As a specific example, I may mention my experience with several biotypes of *Bursa bursa-pastoris* (L.) Britton. These differ from one another by certain characteristic lobings of the leaves, and these characters have proved, on crossing, to be typical Mendelian unit-characters. However, by growing the plants belonging to any of the several biotypes under sufficiently unfavorable conditions they may be made to produce seeds while bearing only the unlobed juvenile type of leaf. The Mendelian rosette characters are then wholly invisible or latent. If the

[10] Toyama, K. Studies on the Hybridology of Insects. I. On some silk-worm crosses with special reference to Mendel's Law of Heredity. *Bull. Coll. Agr. Tokyo Imp. Univ.*, 7, pp. 259–393, pls. VI–XI, July, 1906. See pp. 348–353 and pl. X, III, *a*, *b*, and *c*.

offspring of such plants are grown under favorable conditions the latent characters are again rendered patent, showing that the loss of external manifestation has had no influence upon the allelomorphs themselves; they were present in the badly developed specimens, but were invisible because a sufficiently late stage of differentiation was not attained to permit them to express themselves.

Another striking case in which the latency of a Mendelian character, perhaps due to fluctuation, has been fully demonstrated, is in the cross between blue and white Indian corn investigated by Lock.[11] The blue is, in general, dominant over the white, but the white grains are always in excess of expectation, sometimes more, sometimes less; subsequent breeding tests with the whites show that a sufficient proportion of them are heterozygous, instead of extracted recessives, to make up the deficiency found in the number of blues in the preceding generation. It is not impossible, as Lock suggests, that further investigation of this case will discover some other cause than fluctuation for the latency of the blue aleurone layer in these white-grained heterozygotes.

The classic case of so-called "double adaptation" in *Polygonum amphibium* which is pubescent in its terrestrial form and glabrous when grown as an aquatic, and other cases of the same kind, present illustrations of latency due to fluctuation, instead of being due to the presence of two antagonistic determinants whose activities are mutually exclusive as suggested by De Vries.[12]

The very common occurrence of latency due to fluctuation must have an important bearing upon the significance of cultural conditions for the production of variations. There has been much diversity of opinion on this point, the general impression being that cultivation and the removal of competition are very potent in inducing

[12] De Vries, H. Species and Varieties, their origin by mutation, pp. xviii + 847. 1905. Chicago: Open Court Pub. Co. See p. 430 *et seq.*

[11] Lock, R. H. Plant Breeding in the Tropics. III. Experiments with maize. *Ann. Roy. Bot. Gard. Peradeniya,* 3, pt. 2, pp. 95–184, November, 1906. See pp. 144–163.

variation, and that in consequence of this fact it is improper to apply principles derived under cultivation to plants growing free in nature. There can be no doubt that good cultural conditions render patent many internal characters which are invisible under conditions of poor nutrition and crowding, and this fact together with the fact that many of the common culture-plants are complex hybrids, may fully account for the general impression regarding the effects of culture. There is no satisfactory evidence that good feeding and other conditions usually supplied under tillage have any effect in the production of the mutations upon which the external characters no doubt ultimately depend.

General Considerations

It is obvious from the foregoing results and discussions that latency is not a simple phenomenon, but may be due to a number of different circumstances. The point which I have strongly emphasized in my two preceding papers on the subject of latency—namely, that cases of latency must be explained, not upon the ground of inactivity or dormancy of characteristics, but simply on their invisibility— is fully borne out by all the facts here presented. The several different types depend upon the different causes for the invisibility of the characteristics.

Of the four types of latency here recognized, the first three types—those in which latency is due to definite interrelations between Mendelian units—will give rise to definite characteristic ratios which are as constant for each case as the typical ratios are for typical Mendelian phenomena. This is not so with latency due to fluctuation, as the variable conditions upon which the fluctuations depend may be such that any proportion of the individuals from none to all may have the character in question latent. This is not only true of the characters of pure-bred types as exemplified by *Bursa bursa-pastoris,* but is even more apt to be true of heterozygotes, thus resulting in many deviations from the correct ratios, as

seen in Lock's blue × white corn cross and doubtless in very many other cases.

It is probable that many discrepancies between actual and theoretical ratios are due to some sort of latency. This will generally be detected readily in subsequent generations, and no one should be hasty in declaring that a character which is of the splitting kind is non-Mendelian until the various types of latency are considered which may have taken part in modifying the ratios. "Variable potency," "contamination" or "impurity" of the gametes, and "alternating dominance" will all need to be reconsidered and in some cases reinvestigated, before they can have any secure standing as exceptions, amendments or additions to the simple law of "purity of the gametes" which is the essence of Mendelism.

There is still another way in which unexpected ratios may be produced, without in any way affecting the fundamental principle of the purity of the gametes, their production in equal numbers, and their union according to the laws of chance, and while the question of latency is not involved in this case, it deserves to be mentioned in this connection. Baur[13] has shown that in a variegated race of Antirrhinum, the variegation belongs only to the heterozygote. The extracted recessives are green and the extracted dominants fail altogether to appear, owing evidently to the fact that the zygote so formed is incapable of development, the ratio resulting from self-fertilization of the heterozygotes being therefore 2:1. It is conceivable that every degree of inefficiency of zygotes formed by the union of two particular allelomorphs might occur and thus quite various modifications of the expected ratios be the result, when those ratios are determined by a count of the successful zygotes. This cause for the failure of the expected ratios is certainly of rare occurrence, but like questions of latency it can be demonstrated

[13] Baur, E. Untersuchungen über die Erblichkeitsverhältnisse einer nur in Bastardform lebensfähigen Sippe von *Antirrhinum majus*. *Ber. Deutsch. Bot. Gesell.*, 25, pp. 442–454, 1907.

without difficulty by breeding tests, and these should be made before any new principle is invoked, or the old and well-founded principles are declared invalid, in the attempt to account for such discrepancies.

SUMMARY

The foregoing discussion and conclusions may be summarized thus:

In certain bean hybrids, mottled seed-coats depend upon the presence of a mottling allelomorph in a heterozygous condition, the homozygous condition giving unmottled seeds. This peculiar situation results in a tri-polyhybrid ratio, 18:18:6:6:16, instead of the usual ratio, 27:9:9:3:16.

Latency is held to mean invisibility, and not inactivity or dormancy, and four types are recognized, according to the different causes of invisibility; still other types may be found. The four types discussed in this paper are:

(*a*) *Latency due to separation,* in which an allelomorph when acting alone has no external manifestation and is only rendered patent by combining it with another allelomorph. Such latency gives rise to the ratios 9:3:4, 9:7, 27:9:9:3:16 and 27:9:28, instead of the theoretical, 9:3:3:1 and 27:9:9:9:3:3:3:1.

(*b*) *Latency due to combination,* in which two dominant allelomorphs, each giving rise to a peculiar character when acting alone, lose their external manifestation when co-existing in the same zygote. Upon self-fertilization this type of latency gives rise to such ratios as 1:1, 3:3:2, 18:18:6:6:16, etc., and may be found to account for the existence of certain mid-races, and other cases in which a double series of characteristics are presented in nearly equal numbers.

(*c*) *Latency due to hypostasis,* in which the presence of one allelomorph can not be detected owing to the presence of another allelomorph, the character produced by the latter being unmodified by the activity of the former. This type of latency is exemplified by the black bean

which hides the presence of a wholly distinct brown allelomorph, and a dark orange bean which carries invisibly a light yellow allelomorph. This condition gives rise in one series of crosses to the ratio, 12:3:1. Properly the term "dominance" should be limited to the relation between any positive characteristic and its own absence. Whenever one positive character seems to dominate another positive character, the latter is latent by hypostasis in the individual possessing the former.

(*d*) *Latency due to fluctuation,* a very frequent phenomenon in which characteristics disappear under conditions of poor nutrition, etc. Cultivation under favorable conditions makes such characteristics patent and this fact may account in part for the general impression that cultivation induces variation. Cases of "double adaptation" are examples of this type of latency.

Many discrepancies between theoretical and empirical inheritance-ratios are due to latency, and care should be taken to investigate the possible latencies which may be present before declaring that a character is non-Mendelian, because of a discrepant ratio. "Variable potency," "contamination" or "impurity" of the gametes, and "alternating dominance" which have been proposed to account for the appearance of various novelties, or of deviations from expected ratios, can have no secure standing until the question of latency in the sense of invisibility has been taken into account.

A modification of expected ratios may rarely result also from the failure of certain allelomorphs to make vigorous zygotes when joined together in certain combinations.